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RESEARCH ARTICLE

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Structure and diversity patterns of coralligenous cliffs across three ecoregions in the Central-Western Mediterranean Sea

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Abstract

Aim: Coralligenous reefs are the main marine bioconstructions in terms of spatial distribution within the Mediterranean basin. Two distinct reef morphologies can be distinguished based on the surface and topographical features of the seafloor: cliffs developing vertical slopes and banks found on gently steep or horizontal bottoms. Despite their importance for monitoring and conservation efforts, observations regarding the variability of biogeographical patterns are scarce. Here, we aimed to assess the differences in the composition and structure of these cliffs across ecoregions and estimate the relative role of abiotic environmental features, geographic location, and connectivity in shaping diversity patterns.

Location: The study was carried out in the Central-Western Mediterranean Sea. Samples were collected at 65 sites across the Algero-Provençal Basin, the Ionian Sea and the Tyrrhenian Sea.

Methods: We assessed the composition and structure of coralligenous cliffs through photographic samplings collected by scuba divers. Patterns in α- and β-diversity were associated with 9 abiotic environmental variables, latitudinal and longitudinal gradients, and connectivity measures using Generalized Additive (GAM) and Conditional Autoregressive (CAR) models.

Results: Coralligenous cliffs were primarily composed of algae and displayed a high degree of variability. The Partition Around Medoids (PAM) clustering method successfully delineated seven distinct clusters with a non-uniform distribution within the studied ecoregions. The α-diversity increased in eastern and northern sites and with phosphate concentration, while decreased with temperature, chlorophyll and nitrates concentration. β-diversity at the site level increased with temperature, while it

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was negatively affected by northward current speed and chlorophyll concentration. Moveover, β-diversity increased within connected sites.

Main Conclusions: Coralligenous cliff diversity responds both to the physico-chemical features of the habitat and between-habitats connectivity. However, our findings suggest that small-scale abiotic and biotic processes could contribute to explaining the variability observed. These findings can significantly enhance the monitoring and conservation efforts of this Mediterranean endemic ecosystem.

KEYWORDS
biodiversity, coralligenous cliffs, habitat conservation, Mediterranean Sea, priority habitats, species distribution

1 | INTRODUCTION

Historical legacy, abiotic parameters (i.e., light penetration, water movement, nutrient availability, sedimentation and temperature), connectivity, and the vast array of *intra*- and *inter*-specific relationships between organisms shape biodiversity patterns in marine ecosystems (Gaston et al., 2008). These determinants vary along vertical (bathymetric) and horizontal directions, resulting in significant differences in the structure of biotic assemblages over spatially distinct areas (Adey & Steneck, 2001; Cefalì et al., 2016, 2019; Costello et al., 2017). In the Mediterranean Sea, although the changes in benthic community structure with depth have been historically investigated (i.e., Pérès & Picard, 1964), the biogeographical pattern of community variation represents a new area of study that has recently gained attention (Çinar et al., 2020). Disentangling the contribution of the different factors responsible for the observed patterns is not a trivial task and represents one of the more significant challenges to be faced in this era of unprecedented biodiversity loss (Cefalì et al., 2016; Loreau et al., 2001). Understanding the ecological processes that drive observed patterns requires identifying the appropriate scales of variation: this knowledge is essential for conducting monitoring programmes and environmental state assessments and, furthermore, to effectively enhance the conservation of natural resources (Cefalì et al., 2018; Chase & Leibold, 2002). Furthermore, this aligns perfectly with the principles of the EU's primary tool for protecting and conserving marine waters: the Marine Strategy Framework Directive (MSFD; 2008/56/EC). The ecosystem approach of the MSFD encompasses assessing the spatial variation of benthic communities in response to natural and human-induced gradients (Van Hoey et al., 2010).

The MSFD and the initiatives of the Contracting Parties to the Barcelona Convention, developed within a pan-Mediterranean scenario (UNEP/MAP, 2017), have recently endorsed the development of monitoring, protection and conservation actions focused on one of the endemic ecosystems of the Mediterranean Sea: coralligenous reefs. The term coralligenous identifies biogenic carbonate substrates primarily produced by the accumulation of encrusting red algal thalli (mostly belonging to the orders Corallinales, Hapalidiales and Peyssonneliales; Ballesteros, 2006). These encrusting algae grow in dim light conditions and relatively calm waters, building the reefs with the secondary contribution of sessile animal taxa. Primary and secondary builders create a biogenic substrate that overlays the calcareous remains of previous generations and provides habitats for a wide variety of marine organisms. Among the Mediterranean bioconstructions, coralligenous formations hold significant importance in terms of spatial distribution (Martin et al., 2014), ecological functioning (Ingrosso et al., 2018; Thierry de Ville d'Avray et al., 2019) and commercial value (Zunino et al., 2020). The coralligenous reef distribution spans the entire Central-Western Mediterranean coast, except for the sandy-muddy seabeds of the central Adriatic Sea (Martin et al., 2014), and some areas in the northern Adriatic Sea. These latter are characterized by peculiar biogenic formations known as *tegnùe*, which can be ascribed to mesophotic biogenic habitats rather than to coralligenous reefs, despite the depth range at which they develop (Gianni et al., 2023).

Coralligenous reefs are found between 20 and 130 m of depth, and two distinct morphologies characterize them. This classification is defined by the surface and topographical features of the seafloor hosting the reef: cliffs and banks (i.e., platforms). The former morphology develops on sub-vertical slopes, while the latter is widespread on gently steep or horizontal bottoms, generally below 50 m depth (UNEP/MAP-SPA/RAC, 2021). Such differences result in significant dissimilarities in the structure and composition of coralligenous assemblages (Piazzi et al., 2022).

A distinct feature of coralligenous reefs is the diversity of their assemblages. The recently revised classification of habitat types, proposed by the EUropean Nature Information System (EUNIS), provides a brief but consistent overview of the high diversity and heterogeneity characterizing the assemblages linked to the several facies and associations listed among coralligenous habitats (Montefalcone et al., 2021). The diversity patterns of coralligenous assemblages are scale-dependent and show higher heterogeneity at small spatial scales due to the patchy distribution of sessile organisms (Casas-Güell et al., 2015; Ferdeghini et al., 2000; Piazzi et al., 2004, 2016; Ponti et al., 2011). However, some studies have recently highlighted differences in the structure of coralligenous assemblages among Mediterranean ecoregions or distant areas, confirming the existence of significant patterns on a biogeographical scale (Çinar et al., 2020;

Doxa et al., 2016; Piazzi et al., 2022). Such outcomes were achieved using α- and β-diversity measures and community structure descriptors in the Algero-Provençal basin, the Ionian Sea, and the Aegean Sea. Although these patterns are evident, the determinants have not been clearly identified so far. The hypotheses put forward by the researchers mainly refer to commonly identified drivers, such as geomorphological features (Ponti et al., 2011), temperature (Ceccherelli et al., 2020), connectivity (Bandelj et al., 2020), and anthropic disturbances (Deter et al., 2012; Ferrigno et al., 2018; Piazzi et al., 2017; Sartoretto et al., 2017). Understanding the relative contribution of these abiotic determinants to the observed diversity is increasingly important, particularly for monitoring and conservation purposes, as well as to test and further develop ecological indices (Di Camillo et al., 2023; Gennaro et al., 2020).

This study aims to assess the structure and composition of epibenthic assemblages of coralligenous reefs developing on subvertical substrates (i.e., cliffs). It highlights diversity patterns, identifies the environmental parameters driving such variability, and covers three ecoregions in the Central-Western Mediterranean Sea (Algero-Provençal Basin, Ionian Sea, and Tyrrhenian Sea), encompassing hundreds of kilometres of Italian coasts. We selected observations from these ecoregions to fill a spatial knowledge gap since similar studies were carried out in neighbouring Mediterranean areas (Çinar et al., 2020; Doxa et al., 2016). Here, we want to answer two main questions: (i) what is the composition and structure of coralligenous cliffs in the Central-Western Mediterranean Sea?; (ii) what is the relative role of environmental features, geographic location and connectivity in explaining the patterns of variation in α and β-diversity?

2 | METHODS

2.1 | Study area and sample collection

The study was carried out along the Italian coasts: samples were collected at 65 sites distributed in three out of eight Mediterranean ecoregions (Algero-Provençal Basin, Ionian Sea, and Tyrrhenian Sea; Figure 1, according to Spalding et al., 2007 classification, modified by Giakoumi et al., 2013). Ecoregions, administrative regions, and coordinates of the sampling sites are summarized in Table S1. The sampling unit (SU) consisted of a 4 m^2 area where ten photographs (each covering a surface ≤0.2 m^2) were shot. Three SUs were selected per site, for a total of 195 SUs ($n = 1950$ photographs). A schematic view of the sampling design is shown in Figure S1.

Samples were not balanced among ecoregions because they were gained from different sampling campaigns from 2012 to 2021. In coralligenous cliffs, spatial changes are more substantial than temporal changes (Garrabou et al., 2002; Teixidó et al., 2011), except for positive thermal anomalies and other human-related disturbances (Casoli et al., 2017; Teixidó et al., 2013). Therefore, we adopted a sharing data approach for building a collective database with information coming from different research groups' efforts to cover a broader spatial scale while maintaining a highly detailed resolution in terms of assemblages' composition and structure.

Photographs were taken by SCUBA divers, who sampled between 30 and 35 m, except for Ionian sites where rocky reefs do not extend deeper than 30 m and coralligenous reefs occur in a shallower depth range (25–30 m). Samples were collected during the late spring and early-mid summer months at all sites.

2.2 | Database generation and diversity assessment

The collected pictures were analysed through image analysis software (ImageJ) to gather data on the composition and structure of coralligenous assemblages. As for taxonomic accuracy, image analysis imposes some limitations. Identification was possible to the lowest possible taxonomic level for easily detectable/conspicuous species, whereas organisms not easily recognizable with pictures were assigned to taxonomically and morphologically similar complexes (i.e., morphological groups). Since data came from different research groups, taxonomic accuracy differed, and it was necessary to standardize the dataset following the list of taxa/morphological groups proposed for the assessment of the Ecological Status of Coralligenous Assemblages (ESCA index; Piazzi et al., 2017). This index encompassed a total of 36 sessile taxa/morphological groups, which were further classified into 10 morpho-functional categories based on organisms' taxonomy, generation time and growth form, following the classification adopted by Casas-Güell et al. (2015), Garrabou et al. (1998) and Sini et al. (2019). The list of taxa/morphological groups and their corresponding morpho-functional categories is provided in Table 1.

Coralligenous assemblages were assessed by calculating the percentage cover of the main conspicuous sessile taxa/morphological groups in each picture. Data were unified at the SU level, calculating the mean percentage cover of the photographic replicates to control for the small-scale spatial heterogeneity of the assemblages due to the patchy distribution of organisms (Ferdeghini et al., 2000; Piazzi et al., 2004).

Then, we quantified the diversity of coralligenous assemblages at the SU (α-diversity) and site (β-diversity) levels by using Tsallis entropy (H_q), which is defined as the amount of uncertainty calculated from the frequency distribution of species in a community (Furuichi, 2005). The transformation of entropy measure to diversity measure, or *Hill numbers*, is obtained by taking the deformed exponential transformation e_q of the Tsallis entropy (Marcon et al., 2014). The parameter q within the Tsallis entropy calculation allows tuning H_q in terms of the importance given to rare species: larger values of q put less emphasis on rare taxa. In this study, we selected the diversity of order $q = 1$, which is the Shannon index, corresponding to the standard exponential transformation of H_q. It gives medium importance to rare species; it can be partitioned into independent and significant α and β components when the weights of the communities are unequal (Jost, 2007); and it is appropriate when dealing with

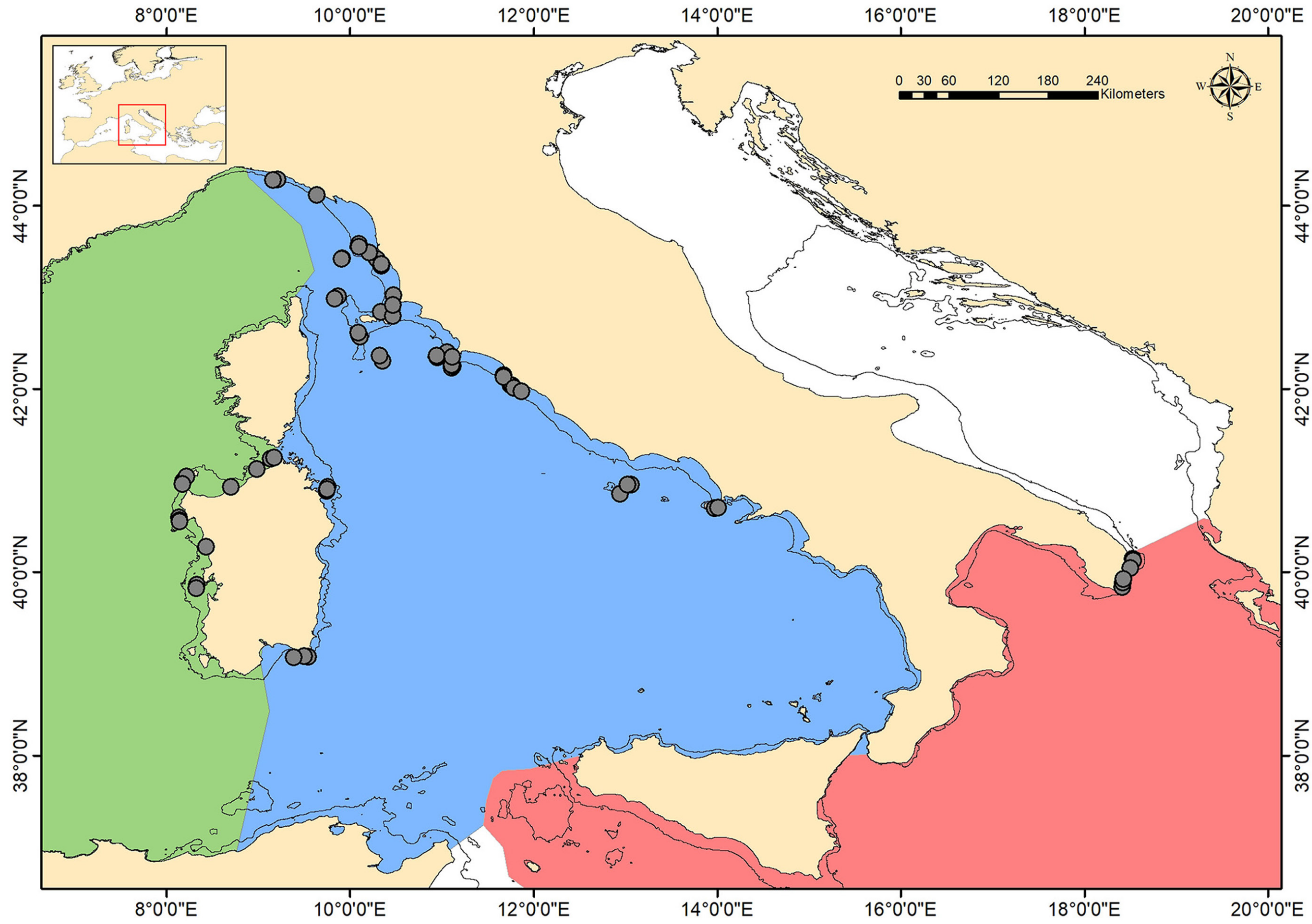

FIGURE 1 Map showing the distribution of the sampling sites (grey dots). The bathymetric contour delineates 100 m of depth (product downloaded from https://ows.emodnet-bathymetry.eu/wfs). Colours highlight the three ecoregions investigated. Green: Algero-Provençal Basin; blue: Tyrrhenian Sea; red: Ionian Sea.

relative abundance data (Anderson et al., 2011; Chao et al., 2010). To estimate H_q, we use the package *entropart* version 1.6-11 developed in the R environment (Marcon & Hérault, 2015).

2.3 | Environmental variables and connectivity assessment

Nine environmental variables were downloaded from the Copernicus Marine Environment Monitoring Service (CMEMS; Escudier et al., 2020; Teruzzi et al., 2021) and used as predictors of α- and β-entropy. The multilevel raster data have a spatial resolution of 1/24° (ca. 5 km) and 16 vertical levels up to 50 m of depth with mean intervals of 3.11 ± 0.93 m. The Copernicus products (MEDSEA_MULTIYEAR_PHY_006_004 and MEDSEA_MULTIYEAR_BGC_006_008) consist of reanalyses integrating models and in situ observations to provide a continuous reconstruction of the past physical and biogeochemical features of the Mediterranean basin (Cossarini et al., 2021). We considered the following variables during a 20-year interval (from 01/01/2000 to 31/12/2020, Table S2): bottom temperature (*T*), salinity (*S*), chlorophyll *a* mass concentration (CHL), phytoplankton carbon biomass (PHYC), dissolved molecular oxygen (DOX), nitrate (NIT) and phosphate (PHO) concentration, and eastward (Es) and northward (Ns) current speed. After downloading the raster, we extracted variable values for each of the 65 sites. Daily values were averaged over the entire study period (2000–2020) and over the depth interval between 26.20 and 37.85 m. This specific bathymetric range corresponds to the range of occurrence of the investigated coralligenous cliffs. Although the approach has limitations, especially in detecting local variation, the long-term temporal averaging calculation was adopted to characterize climatologically and environmentally the study sites and cope with the differences in the underwater sampling times, according to the approach carried out by Rattray et al. (2016) in a similar study.

Connectivity was represented by assigning each of the 65 investigated sites to the clusters of areas connected by marine currents by Andrello et al. (2015). Briefly, these authors used a biophysical model to simulate larval dispersal by marine currents over the entire Mediterranean coastal areas (0–200 m of depth) using a grid size of 0.1° × 0.1°. Then, they used the connectivity matrix as input to the splitting algorithms of Nilsson Jacobi et al. (2012), which return a classification of coastal areas into discrete connectivity clusters

TABLE 1 List of the 36 sessile taxa/morphological groups and corresponding morpho-functional categories considered in the study of the composition and structure of coralligenous assemblages. The ID code was used to improve the readability of the graphical representation of the data.

Sessile taxa/morphological groups	ID	Morpho-functional categories
Encrusting calcareous Rhodophyta (Corallinales)	ENCO	Perennial algal encrusting (PAEn)
Encrusting Ochrophyta [e.g. *Zanardinia typus* (Nardo) P.C.Silva, 2000]	ENOC	
Palmophyllum crassum (Naccari) Rabenhorst, 1868	PACR	
Peyssonnelia spp.	PEYS	
Valonia spp.	VALO	
Articulated calcareous Rhodophyta (Articulated Corallinales)	ARCO	Perennial algal erect (PAEr)
Codium spp.	CODI	
Dyctiotales	DYCT	
Erect corticated terete Ochrophyta [e.g. *Sporochnus pedunculatus* (Hudson) C.Agardh, 1817]	EROC	
Erect corticated terete Rodophyta [e.g. *Osmundea pelagosae* (Schiffner) K.W.Nam, 1994]	ERRH	
Flabellia petiolata (Turra) Nizamuddin, 1987	FLPE	
Flattened Rhodophyta with cortication (e.g. *Kallymenia* spp.)	FLRH	
Fucales and Tylopteridales [e.g. *Cystoseira* spp., *Sargassum* spp., *Phyllariopsis brevipes* (C.Agardh) E.C.Henry & G.R.South, 1987]	FUCA	
Halimeda tuna (J.Ellis & Solander) J.V.Lamouroux, 1816	HATU	
Caulerpa cylindracea Sonder, 1845	CACY	Perennial algal turf (PATu)
Filamentous and Siphonous with separate filaments Chlorophyta *[Cladophora* spp., *Pseudochlorodesmis furcellata* (Zanardini) Børgesen, 1925]	PSFU	
Algal turf	ALTU	Seasonal algal turf (SATu)
Perforating sponges (e.g. *Cliona* spp.)	PESP	Perennial invertebrates boring (PIBo)
Azooxantellate individual scleractinians (e.g. *Leptopsammia pruvoti* Lacaze-Duthiers, 1897)	AZSC	Perennial invertebrates cup (PICu)
Zooxantellate colonial scleractinians [e.g. *Cladocora caespitosa* (Linnaeus, 1767)]	ZOSC	
Encrusting ascidians	ENAS	Perennial invertebrates encrusting (PIEn)
Encrusting bryozoans	ENBR	
Encrusting sponges	ENSP	
Large serpulids [e.g. *Salmacina/Filograna* complex, *Protula tubularia* (Montagu, 1803), *Serpula vermicularis Linnaeus, 1767]*	SERP	
Parazoanthus axinellae (Schmidt, 1862)	PAAX	
Erect ascidians	ERAS	Perennial invertebrates massive (PIMa)
Prostrate and massive sponges [e.g. *Chondrosia reniformis* Nardo, 1847, *Petrosia ficiformis* (Poiret, 1789), *Agelas oroides* (Schmidt, 1864), *Acanthella acuta* Schmidt, 1862]	PMSP	
Adeonella calveti Canu & Bassler, 1930, *Reteporella* spp., *Smittina cervicornis* (Pallas, 1766)	REGR	Perennial invertebrates tree (PITr)
Arborescent sponges (e.g. *Axinella polypoides* Schmidt, 1862)	ARSP	
Corallium rubrum (Linnaeus, 1758)	CORU	
Eunicella cavolini (Koch, 1887), *Savalia savaglia* (Bertoloni, 1819), *Leptogorgia sarmentosa* (Esper, 1791)	EUNI	
Myriapora truncata (Pallas, 1766)	MYTR	
Paramuricea clavata (Risso, 1827)	PACL	
Pentapora fascialis (Pallas, 1766)	PEFA	
Hydrozoans (e.g. *Eudendrium* spp.)	HYDR	Seasonal invertebrates turf (SITu)
Ramified bryozoans [e.g. *Caberea boryi* (Audouin, 1826), *Cellaria fistulosa* (Linnaeus, 1758)]	RABR	

found by favouring clustering of grid points connected by sufficiently large larval dispersal probabilities. Different numbers of clusters can be found by varying the level of larval dispersal needed to include two grid points in the same cluster. Here, we used the two extreme clusterings among those obtained by Andrello et al. (2015), corresponding to 9 and 33 clusters at the Mediterranean basin scale. The 65 investigated sites were categorized into 3 and 5 clusters based on the aforementioned clustering (Figure 2).

Furthermore, we estimated proximity between pairs of sites i, j ($d_{i,j}$) by calculating the Euclidean distance around barriers (i.e., land) through the function "gridDistance" within the *raster* package version 3.6-20 in R. The Euclidean distances around barriers were used to weigh the connectivity matrix as follows:

$$C_{i,j} / \sqrt{d_{i,j}}$$

If the sites i and j belong to the same connectivity cluster, $C_{i,j}$ is assigned a value of 1; otherwise, it has a value of 0. The variable $d_{i,j}$ is the Euclidean distance around barriers between each pair of sites. We hypothesize that the proximity between pairs of sites may contribute to enhancing spatial structure in modelling β-diversity at individual sites.

2.4 | Statistical analyses

We adopted the Partition Around Medoids (PAM) clustering method (Kaufman & Rousseeuw, 1990) to group the 195 SUs according to the structure of coralligenous cliffs based on taxa/morphological groups percentage cover. The PAM was performed on a dissimilarity matrix calculated on the Bray–Curtis dissimilarity index. The selection of the optimal number of clusters ($k=7$, Figure S2) was carried out using the average silhouette width criterion (Rousseeuw, 1987). The silhouette score serves as a measure for assessing the quality of clustering and ranges from −1 to 1. For each SU, the difference between the mean *intra*-cluster distance to which it belongs and the mean *intra*-cluster distance of the closest clusters is calculated. A positive value indicates a correct assignment, while a negative value indicates an incorrect position. The number of clusters selected corresponds to the number of groups generated by the partition that obtained the greatest width of the silhouette average for the entire dataset, i.e., the average of the silhouette coefficient of all the observations. The partitioning was carried out through the "pam" function in R package *cluster* version 2.1.4. The clusters highlighted through PAM were mapped, and for interpretation of the dissimilarities between clusters, a Principal Coordinates Analysis (PCoA) based on Bray–Curtis dissimilarity was applied. The taxa/morphological groups' abundance was visualized according to the cluster they belong to by using the "MetaCommunity" function in the *entropart* package (Marcon & Hérault, 2015). The weighted average probabilities of occurrence of taxa/morphological groups and their abundance (i.e., percentage cover) define the metacommunity as the assemblage of communities.

A correspondence analysis (CA) was performed to assess the structure of coralligenous assemblages according to the three investigated ecoregions. The data were not transformed since they were uniformly reported as percentage cover. The CA was performed using the function "cca" within the R package *vegan* version 2.6-4.

The calculation of α- and β-diversity was performed using the "DivPart" function within the *entropart* package. The results provide information on the Shannon index at the SUs' level (α-diversity) and at the site level (i.e., β-diversity as a single value per site). Environmental variables were scaled to facilitate comparison of effect sizes, and their correlation was calculated (Figure S3). We deleted PHYC because it was largely correlated with CHL; the other predictors were retained, despite the strong correlation between some of them, when estimating the statistical models to help the ecological interpretation.

Generalized additive models (GAMs) were used to test the non-linear response of the α and β-diversity to environmental covariates and the geographical coordinates expressed as decimal degrees in WGS 84. AIC and BIC criteria were used to select the best combination of covariates and find the optimal model; the goodness of fit was measured as the percentage of deviance explained and adjusted pseudo-R^2. GAMs allow for both linear and non-linear relationships between the response variable and multiple explanatory variables. We used restricted maximum likelihood (REML) for smoothing parameter selection, following Wood (2011). To consider the dependence of β-diversity on spatial location and connectivity pattern (Andrello et al., 2015), we used tensor products weighted by connectivity clusters (Wood, 2006). GAMs were estimated using the "gam" function of the R package *mgcv* version 1.8-42 (Wood & Wood, 2015).

Furthermore, we used a Conditional Auto-Regressive (CAR) approach to account for the spatial correlation among observations across the different sites (Schmidt & Nobre, 2014; Ver Hoef, Peterson, et al., 2018) when modelling the β-diversity as a function of the explanatory variables. This approach enables us to effectively discuss the pattern of β-diversity, assuming a specific structure for the spatial dependence defined by connectivity clusters. Further details are reported in Table S4.

To meet all the assumptions, the dependent variables were log-transformed; therefore, both α- and β-entropy were considered in the models' estimation; a level of significance of 0.05 (p-value <.05) was selected.

3 | RESULTS

3.1 | Characterization of the coralligenous cliffs

The characterization of the coralligenous cliffs performed through PAM revealed seven clusters; each of them was composed of samples with a similar percentage cover of taxa/morphological groups and, therefore, similar composition and structure of the assemblages. The PCoA plot shows the degree of similarity between the

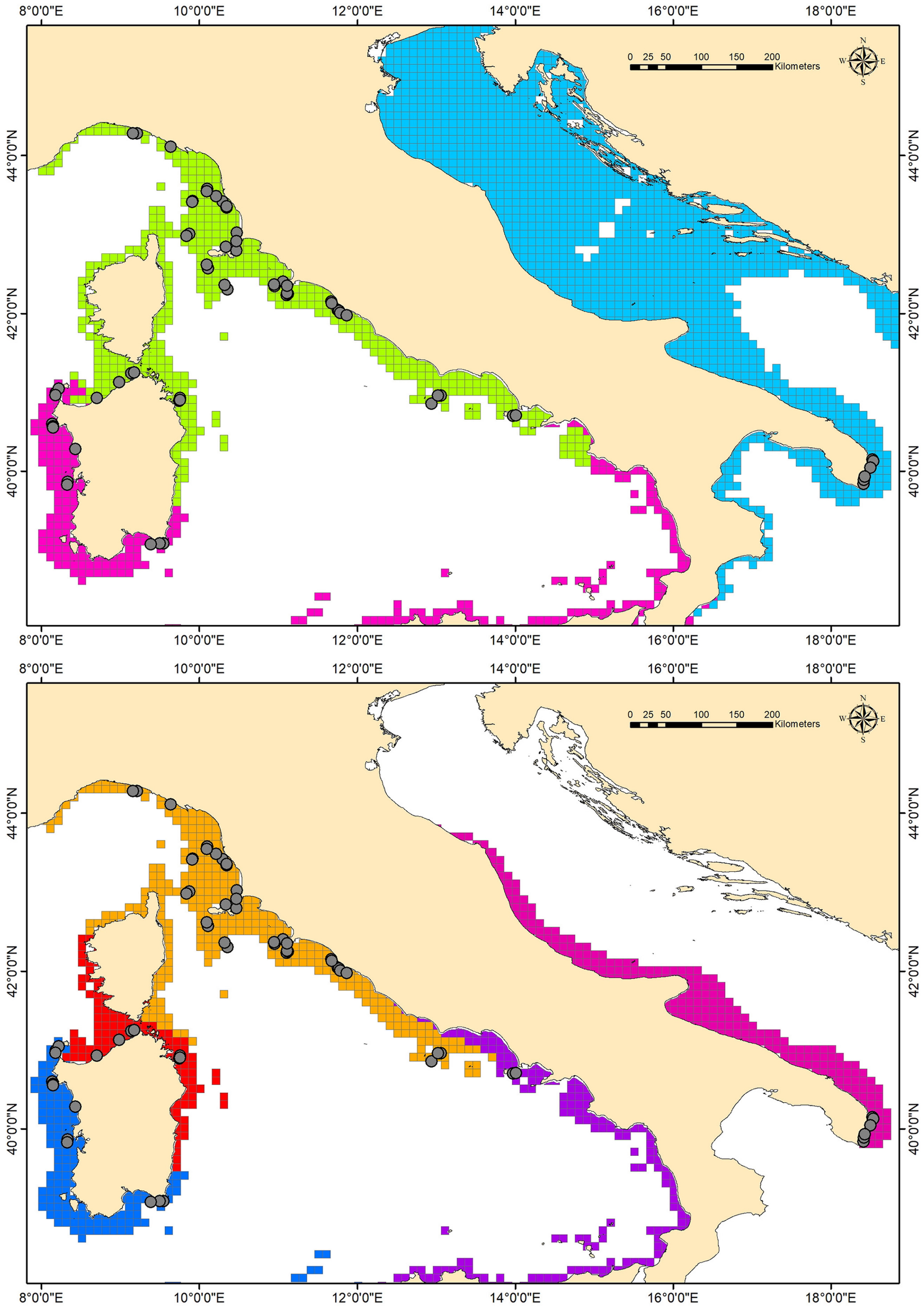

FIGURE 2 Site distribution and the relative connectivity clusters corresponding to the two extreme clusterings identified by Andrello et al. (2015), corresponding to 9 (upper panel) and 33 (lower panel) clusters at the Mediterranean basin scale. The colours match those shown in Figure 4 provided by Andrello et al. (2015).

assemblage clusters for each SU (Figure 3a): the observations of CL2 and CL6 showed low dispersion if compared to the more heterogeneous CL1, CL3, CL4 and CL5. The average silhouette value of the PAM clustering was low (0.37) and reflected the heterogeneity of the data: the number of SUs per cluster (ranging from 7 in CL7 to 63 in CL2) and the *intra*-cluster silhouette varied among the six clusters (Figure 3b). The highest mean silhouette values were reported for CL4 (0.57 ± 0.10, mean ± SD), CL2 (0.54 ± 0.16), and CL7 (0.52 ± 0.21), encompassing 9, 63, and 7 SUs, respectively. CL1 (0.12 ± 0.13) and CL5 (0.21 ± 0.15) were the most heterogeneous conditions, containing 42 and 12 SUs, respectively, thus significantly impacting the average silhouette value. Negative values characterized some of the observations belonging to CL1, which therefore can be identified as a residual cluster encompassing SUs with less degree of consistency.

Algae dominated in terms of percentage cover in all the assemblage clusters except for CL7 (Figure 3c), in which invertebrates reached mean values of 70 ± 10%. Perennial taxa were the most abundant in the investigated coralligenous assemblages, whereas seasonal taxa contributed to biotic cover for less than 10%; in CL3 exclusively, the seasonal algal turf exceeded 40% of percentage cover. Perennial encrusting algae (mostly belonging to Corallinales, Hapalidiales and Peyssonneliales) represented the most abundant morpho-functional category structuring the epibenthic assemblages in four out of the seven identified clusters (65 ± 16% in CL1, CL2, CL3 and CL6). Among perennial encrusting algae, Peyssonneliales exhibited higher percentage cover values than Corallinales in CL6 exclusively. The erect algae showed an opposite pattern if compared to the encrusting algae and displayed inconsistent but considerable percentage cover values exceeding 10% in CL1, CL4, CL5 and CL6. However, the composition of perennial erect algae varied among clusters and was represented mainly by *H. tuna* together with erect Rhodophyta and Ochrophyta in CL1, *S. pedunculatus*, *Sargassum* sp., and *Cystoseira* spp. (*sensu lato*) in CL4, *F. petiolata* and *H. tuna* in CL5, whereas Dictyotales and erect Rhodophyta characterized CL6. Encrusting (mostly bryozoans and sponges) and erect (i.e., trees belonging to the following taxa: the bryozoans *A. calveti*, *M. truncata*, *P.*

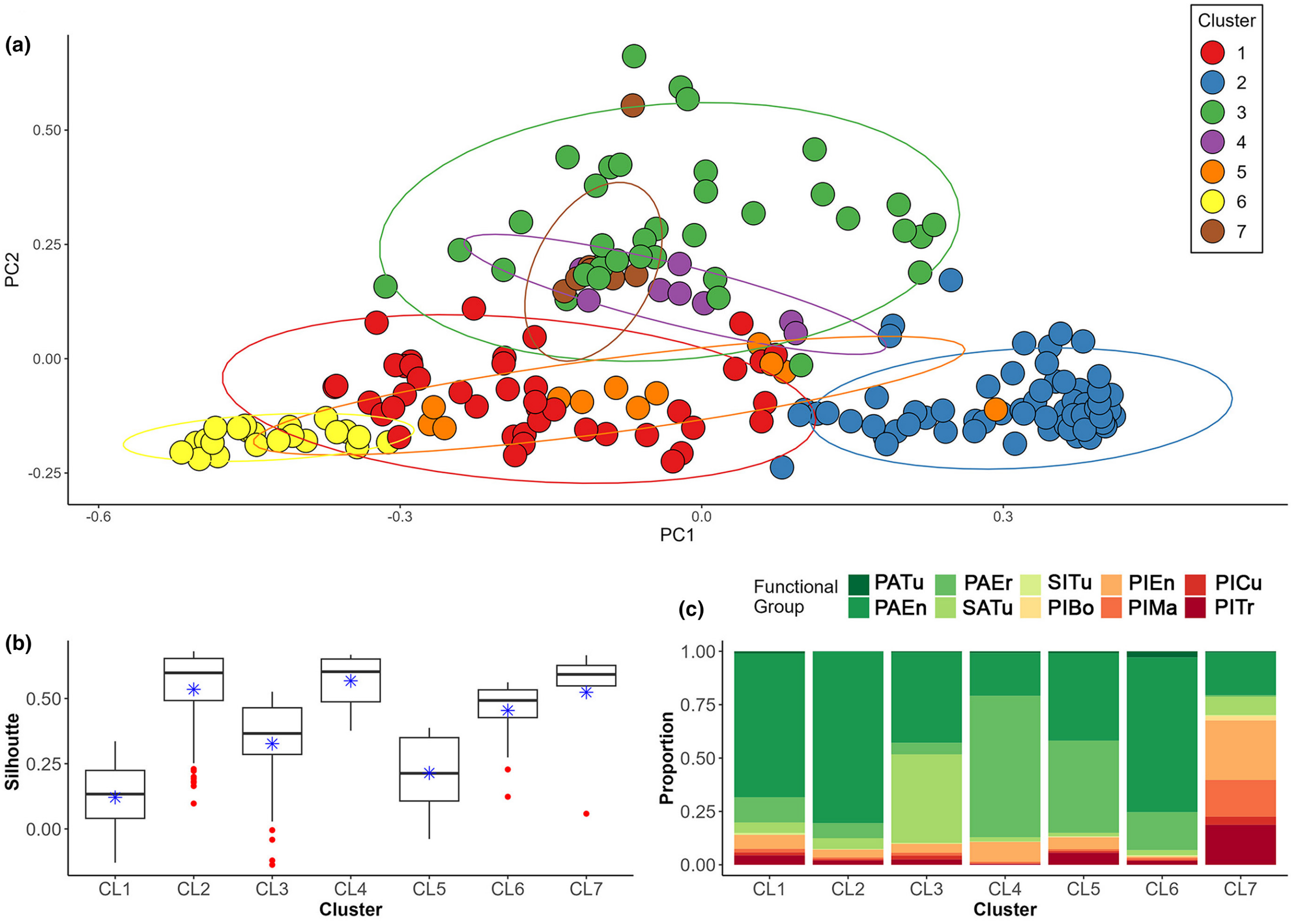

FIGURE 3 Features of the assemblage clusters identified by the composition and structure of coralligenous epibenthic assemblages. (a) Principal Coordinates Analysis (PCoA) plot of the 7 PAM (Partitioning Around Medoids) clusters: dots indicate sampling units (SUs, $n = 195$). (b) Intra-cluster silhouette values, with blue asterisks indicating the mean values per cluster and red dots indicating outliers. (c) The structure of the seven assemblage clusters is described by the mean percentage cover of the algal (highlighted through the green colour palette) and invertebrate (indicated by the red colour palette) morpho-functional categories used to summarize the information about taxa/morphological groups. Acronyms used to indicate morpho-functional categories are specified in Table 1.

fascialis, *Reteporella* spp. and *S. cervicornis*, and the octocorals *C. rubrum*, *E. cavolini* and *P. clavata*) invertebrates did not exceed 10% and 5% of substrate covered, respectively (5 ± 2% and 3 ± 2%) in clusters CL1-CL5. The contribution of invertebrate taxa was very limited in CL6, where perennial erect taxa (the erect bryozoans *P. fascialis* and the octocoral *E. cavolini*) were mostly responsible for covering less than 2% of the substrate. Encrusting, massive and erect invertebrates significantly contributed to structuring the CL7 assemblage cluster, with 28 ± 8%, 17 ± 7% and 19 ± 3%, respectively. Encrusting and massive sponges [*A. oroides*, *Aplysina cavernicola* (Vacelet, 1959), *Chondrilla nucula* Schmidt, 1862, *Haliclona fulva* (Topsent, 1893), and *Hexadella pruvoti* (Topsent, 1896)], erect bryozoans (*M. truncata*, *Reteporella* spp., and *S. cervicornis*), the octocoral *P. clavata*, and encrusting ascidians were the taxa/morphological groups mainly responsible for this pattern.

The detailed structure of the assemblage (reported by taxa/morphological group) *per* cluster and the contribution of each cluster to the definition of the metacommunity of the coralligenous assemblages in the Central-Western Mediterranean Sea are reported in Table S3. The clusters CL1, CL2, CL3, and CL6 mostly contribute to characterizing the metacommunity within the study area, representing approximately 85% of the observations.

3.2 | Spatial distribution patterns of the epibenthic coralligenous assemblages

The distribution of the seven clusters in the study area was not uniform, as depicted in Figure 4. The observations along the coasts of Sardinia (Figure 4a) were extremely diversified, with six of the seven clusters identified. As for the sites belonging to the Algero-Provençal ecoregion, CL1 characterized most of the areas along the western coasts of the island, whereas a higher prevalence of both CL1 and CL2 was reported for observations located along the northern side. These two clusters characterized Sardinian sites within the Tyrrhenian ecoregion, although high heterogeneity within sites was reported in the north-eastern sector. CL2 and CL3 mainly defined the northern part of the Tyrrhenian basin (Ligurian Sea and Tuscan Archipelago, Figure 4b–d), except for some observations belonging to CL1, CL4, CL5 and CL6 (the islands of Capraia, Giglio, Giannutri, Gorgona and Montecristo, localized in the western and southern parts of the Tuscan Archipelago). In particular, CL4 exhibited a uniform distribution compared to the other clusters, identifying 9 different SUs that were situated in Montecristo and Sardinia's northwest sector (Asinara island). The six sites in the central Tyrrhenian Sea that are closely situated to each other revealed similar assemblages, with all of them categorized as CL3 uniformly (Figure 4e). The *intra*-site homogeneity was high in the central-southern areas of the Tyrrhenian ecoregion, which was predominantly assigned to CL5 and CL7 (Figure 4f). In contrast, CL6 dominated consistently across the Ionian Sea ecoregion except for the site located at its northernmost part, corresponding to cluster CL1 (Figure 4g); all the Ionian SUs were uniformly categorized into a single cluster *per* site.

The ordination of SUs along the first two axes of the CA showed the presence of two distinct groups, one formed by Algero-Provençal and Tyrrhenian samples and the other including Ionian samples (Figure S4). The analysis proved the high variability of the dataset, as the cumulative percentage of variance explained by the taxa/morphological group data for the first two axes was quite low, 32.6% (18.8% for axis I and 13.8% for axis II).

3.3 | Environmental features and connectivity shape diversity patterns

α- and β-entropy values, calculated at the site level, are shown in Supplementary Materials (Figure S5), while the GAM output is reported in Table 2. The portion of explained deviance and the pseudo-R^2 were 68.4% and 0.649, and 54.1% and 0.41, respectively. The α-entropy (Figure 5), which is measured by Shannon's index at the SU level, decreased with temperature (*T*) and concentration of nitrates (NIT), although the latter variable showed a level of marginal statistical significance ($p < .10$). On the other hand, a positive relationship was found between both longitude (X-UTM) and eastward current speed (Es) and α-entropy. GAM illustrated fluctuating patterns for the relation between α-entropy and salinity (*S*), with a dependent variable increase at maximum *S* values. The α-entropy (and hence the diversity) exhibited an inverse sigmoid trend regarding chlorophyll concentration (CHL), resulting in a decrease for the SUs where CHL values were highest. Conversely, α-entropy increased almost linearly with phosphate concentration in seawater (PHO). Furthermore, according to the latitudinal gradient (Y-UTM), α-entropy showed a U-shaped pattern, with higher values reported predominantly in the northern part of the study area.

Environmental features showed a linear relationship exclusively with the β-entropy (Figure 6a): the dependent variable, measured at the site level, increased with *T*, although the predictor exhibited a level of marginal statistical significance ($p < .10$). On the contrary, northward current speed (Ns) and CHL had a negative and significant effect on β-entropy, while NIT and concentration of phosphates (PHO) displayed a non-significant effect on the dependent variable. The smoothing effect of longitude (X-UTM) and latitude (Y-UTM) showed two different patterns according to connectivity clusters (Figure 6b): the smoothing gradient highlighted a positive effect on β-entropy as both X-UTM and Y-UTM decreased for the observation included in the connectivity cluster of the Tyrrhenian Sea. β-entropy from the Ionian Sea and the Algero-Provençal Basin showed an opposite pattern but were consistent with each other. Higher and significant changes were reported for observations belonging to the connectivity cluster located in the Algero-Provençal Basin.

The spatial structure (neighbourhoods) adopted in the CAR model was the lower extreme clustering among those obtained by Andrello et al. (2015), corresponding to 9 connectivity clusters at the Mediterranean basin scale and 3 clusters in our study region (upper panel in Figure 2). AIC, BIC and pseudo-R^2 used for the model selection are reported in the Supplementary Materials (Table S4). The choice of weighing

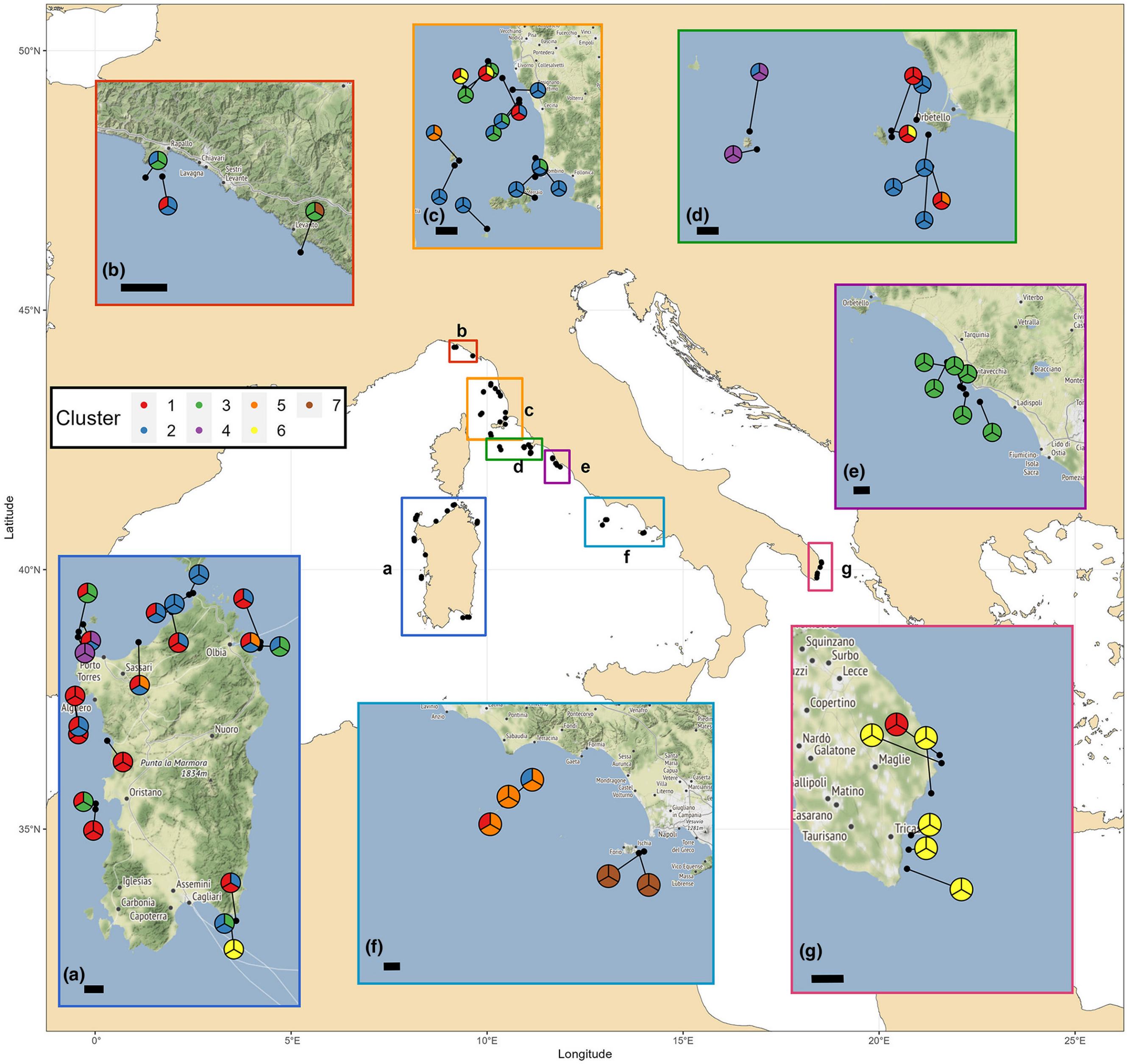

FIGURE 4 Spatial distribution patterns of the seven assemblage clusters identified through PAM: each SU has been associated with the cluster it belongs to and highlighted by using the same colours displayed in the PCoA plot. To enhance the clarity and understanding of the map and distribution patterns, we opted to magnify the areas where observations were concentrated: (a) the whole Sardinia island, facing both Algero-Provençal and Tyrrhenian Sea ecoregions; (b) the Ligurian Sea; (c, d) the central-northern and southern parts, respectively, of the Tuscany coasts and Tuscan Archipelago; (e, f) central and central-southern Tyrrhenian Sea, corresponding to the northern part of Latium and Pontine and Ischia islands, respectively; (g) the eastern coast of Apulia, encompassing the observations located in the Ionian Sea ecoregion. Scale bars in the magnified maps indicate 10 km.

the connectivity between sites using the Euclidean distance around barriers did not improve the estimates of the models for the β-entropy. The presence of a spatial dependence was confirmed by the estimation of the spatial autoregression coefficient λ ($\lambda = -2.93$; p-value = .049), which allowed us to reject the null hypothesis (H_0: $\lambda = 0$, no spatial dependence). However, $\lambda < 0$ revealed a negative spatial autocorrelation, meaning that the connectivity cluster hosts differently diversified sites and therefore the β-entropy at the site level is not concordant within the cluster. The output of the CAR model is reported in Table S5.

4 | DISCUSSION

In the present study, we investigated the structure and composition of coralligenous assemblages colonizing cliffs over a broad spatial scale in the Central-Western Mediterranean Sea and the role of environmental factors in shaping the diversity patterns. The communities exhibited a high degree of variability even if surveyed using photographic sampling techniques, which imposed some limitations on species identification and tended to underestimate the presence of organisms within crevices.

TABLE 2 Output of the GAM on α and β-entropy, reporting the model's linear and non-linear terms. Significant *p*-values, at the selected significance level of .05, are highlighted in bold. The acronyms of the environmental variables, as reported in Table S2 (ID) and cited in the manuscript, are included in brackets.

α-entropy				
Linear terms				
Explanatory variable	**Estimated coefficient**	**St. error**	***t*-value**	***p*-value**
Intercept	11.249	3.697	3.043	**.002**
Temperature (*T*)	−10.317	3.692	−2.794	**.005**
Eastward current speed (Es)	0.171	0.038	4.408	**<.001**
Mole concentration of nitrate in sea water (NIT)	−1.065	0.593	−1.795	.074
Longitude (XUTM)	1.400	0.699	2.002	**.047**
Non-linear (smooth) terms				
Explanatory variable	Estimated df	Reference df	F	p-value
Salinity (sS)	8.163	8.678	9.321	**<.001**
Mass concentration of chlorophyll a in sea water (sCHL)	2.500	3.156	3.830	**.014**
Mole concentration of phosphate in sea water (sPHO)	2.338	2.781	6.852	**.001**
Latitude (sYUTM)	2.525	2.951	4.337	**.003**
Deviance explained = 68.4%; pseudo-R^2 0.649				
β-entropy				
Linear terms				
Explanatory variable	Estimated coefficient	St. error	t-value	p-value
Intercept	−1.942	1.796	−1.081	.284
Temperature (*T*)	3.129	1.767	1.770	.083
Nitrate concentration (NIT)	−0.183	0.443	−0.412	.682
Phosphate concentration (PHO)	0.133	0.352	0.377	.708
Northward current speed (Ns)	−0.083	0.029	−2.843	**.006**
Chlorophyll a mass concentration (CHL)	−0.780	0.246	−3.176	**.003**
Non-linear (smooth) terms				
Explanatory variable	Estimated df	Reference df	F	p-value
XUTM,YUTM: Tyrrhenian Sea cluster (green in Figure 2a)	3.000	3.000	0.617	.607
XUTM,YUTM: Ionian Sea cluster (sky blue in Figure 2a)	2.000	2.000	1.102	.340
XUTM,YUTM: Algero-Provençal Basin cluster (purple in Figure 2a)	4.261	4.828	5.590	**<.001**
Deviance explained = 54.1%; pseudo-R^2 0.410				

However, such an approach enabled researchers to manage several limitations always occurring when sampling coralligenous cliffs, such as time, depth, operational and conservation issues (Piazzi et al., 2019; Zapata-Ramírez et al., 2013), and to work at the coarsest possible taxonomic levels without altering the diversity patterns (Çinar et al., 2020). The identification of discrete clusters through PAM allowed us to handle the high heterogeneity of the assemblages without overlooking the variability within each discrete entity and explicitly visualizing the spatial distribution patterns of coralligenous communities. From the descriptive analyses, different patterns emerged among ecoregions. This represents a further development of the work that will need to be tested in the future using more robust inferential approaches. Our models suggest that the large-scale diversity patterns resulted from environmental features, geographic location, and connectivity influences. The model used to describe this pattern did not benefit from quantifying the distance between sites when accounting for spatial correlation. However, small-scale abiotic and biotic processes (i.e., disturbance, topographic heterogeneity and the vast array of biological interactions) that were not considered in the present study may interplay and significantly contribute to the variability observed.

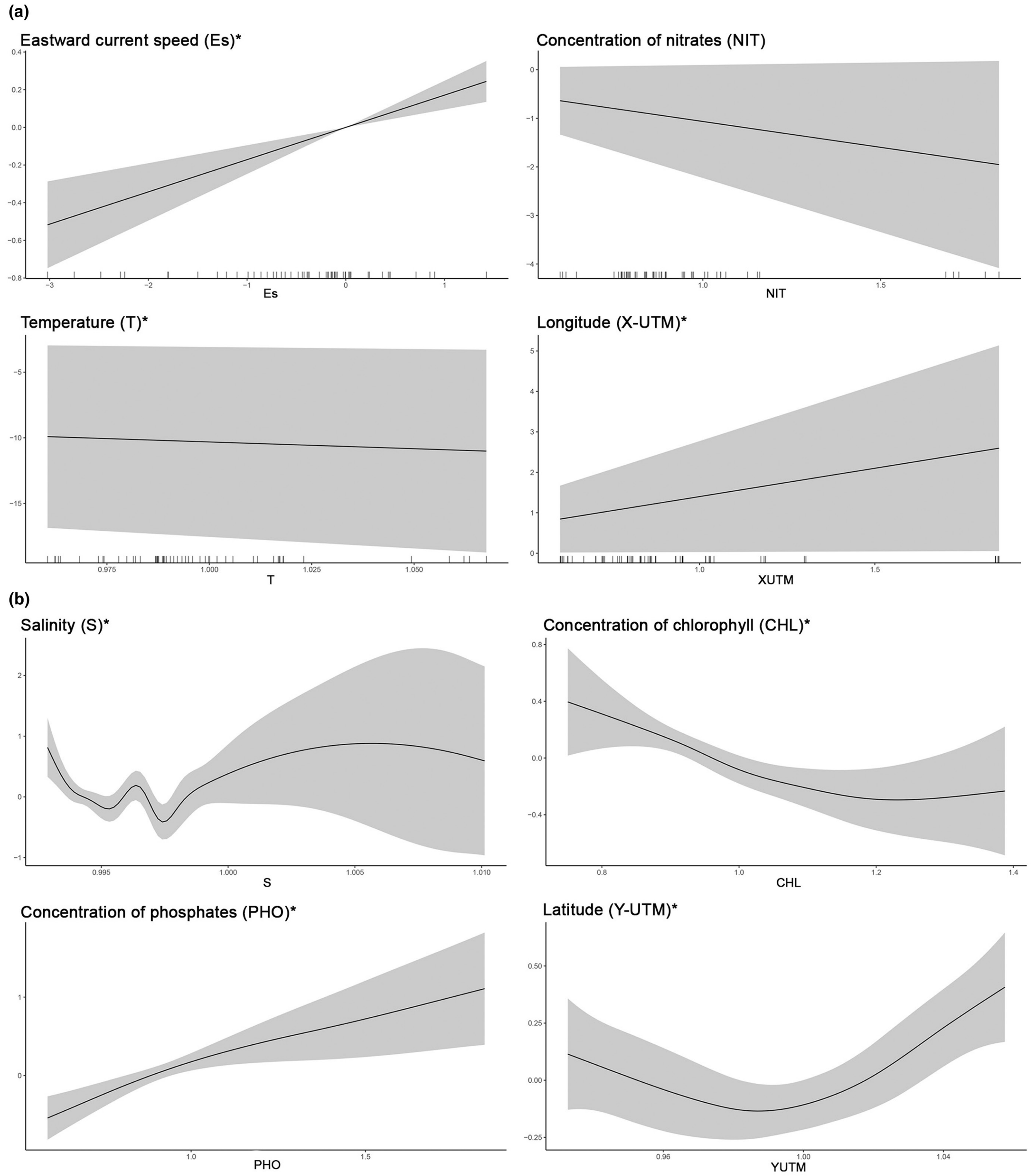

FIGURE 5 Response curves of the α-entropy (*Y*-axis) to environmental variables and the geographical coordinates in the GAM analysis. Both linear (a) and smoothed (b) terms are reported; significant terms are noted with an asterisk and the grey area indicates the 95% confidence interval. The *X*-axis reports the scaled values of the environmental variables.

4.1 | Coralligenous as a community puzzle

The structure of shallow (<40m of depth) coralligenous cliffs in the Central-Western Mediterranean Sea offers insights into an alternative perspective to the common iconography characterized by the presence of erect invertebrates, whose exuberance shades the other components of the assemblage. Algae dominated, in terms of percentage cover, in six of the seven clusters (CL1–CL6) identified

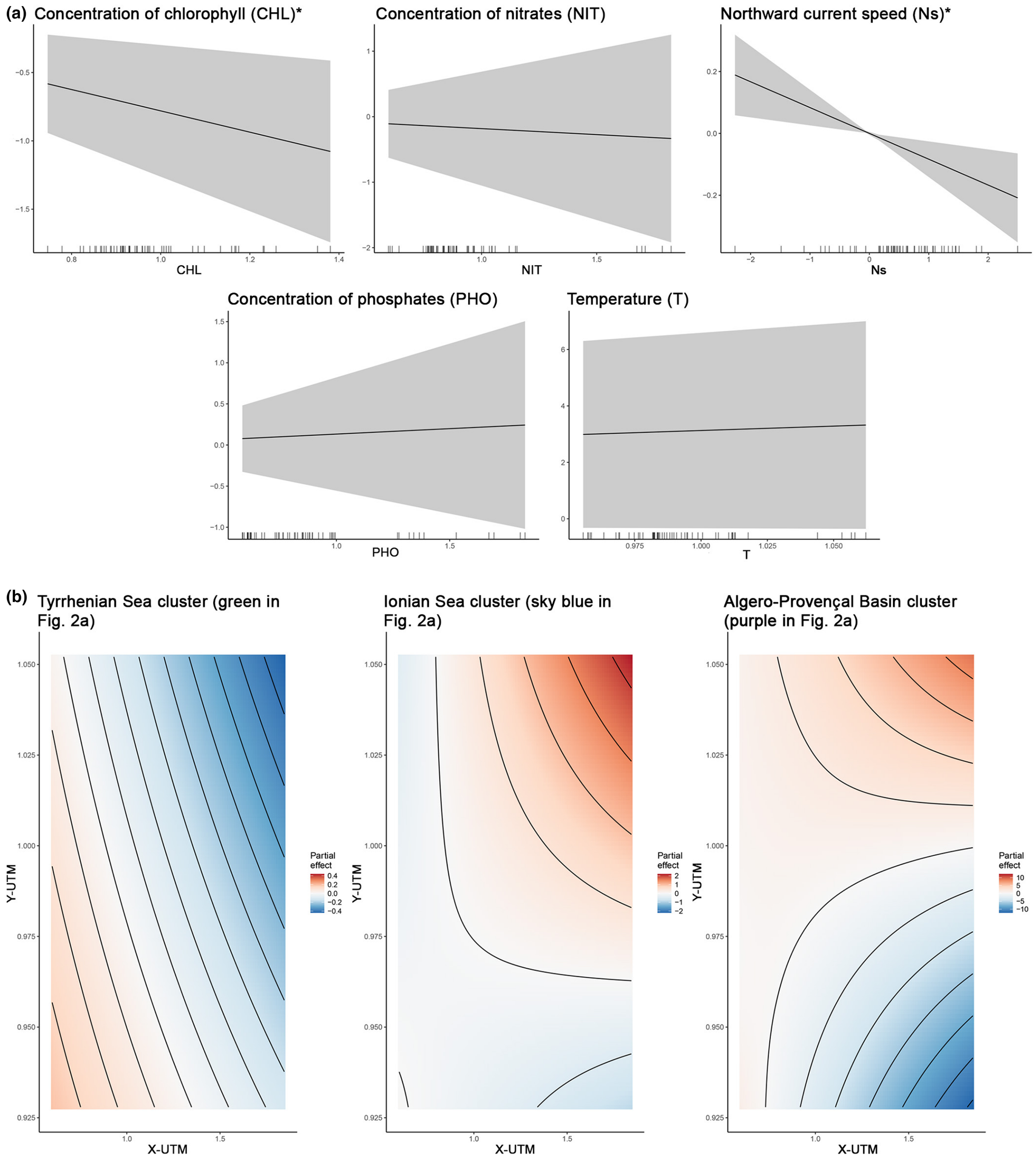

FIGURE 6 Response curves of the β-entropy (*Y*-axis) to environmental variables and the geographical coordinates in the GAM analysis. Both linear (a) and smoothed (b) terms are reported; significant terms are noted with an asterisk and the grey area indicates the 95% confidence interval. The *X*-axis reports the scaled values of the environmental variables.

through the PAM; in particular, algal taxa structured at least two among encrusting, intermediate and erect layers (according to Gatti et al., 2015) in CL4–CL6. The encrusting red algae (Corallinales, Hapalidiales and Peyssonneliales), the percentage cover of seasonal turf algae, and the erect algal taxa characterized the above-mentioned six clusters. Given their role as primary builders within the reef (Ballesteros, 2006), encrusting red algae are the most abundant taxonomic/morphological group in all sectors of the Mediterranean (Çinar et al., 2020; Piazzi et al., 2010; Sini et al., 2019). The clusters CL1 and CL2 reflected the accepted stratified structure and general features of Western Mediterranean coralligenous assemblages (Casas-Güell et al., 2015; Casoli et al., 2020; Çinar et al., 2020; Gatti et al., 2015; Kipson et al., 2011; Piazzi et al., 2021), where encrusting red algae form the basal layer, bryozoans dominate the intermediate layer and anthozoans (*C. rubrum*, *E. cavolini*, *P. clavata*) create the upper layer. These clusters characterized 59.9% of the observations from the Algero-Provençal and Tyrrhenian basins, reinforcing the pattern reported by the aforementioned studies.

The percentage cover of turf and erect algae characterizing CL3–CL6 highly differed from those described in both the western and eastern sectors of the Mediterranean Sea, with the sole exception to this trend reported in the Gulf of Lions (Méjean, a few km east of the Rhône mouth, Çinar et al., 2020). The occurrence and abundance of seasonal algal turfs often indicate disturbed conditions (Montefalcone et al., 2017; Piazzi et al., 2011, 2012). Indeed, CL3 is localized in the close proximity of the area affected by the Tiber River run-off or along the strongly urbanized coastal areas of the central and northern Tyrrhenian Sea (Piazzi et al., 2023; Pierdomenico et al., 2021). Turf algae are well adapted to altered environmental conditions, efficiently trapping sediment and rapidly recovering from disturbances, so that their increasing trend at the expense of canopy-forming assemblages has been globally reported (Connell et al., 2014). On the contrary, the high percentage cover of brown (*S. pedunculatus*, *Sargassum* sp., and *Cystoseira* spp. *sensu lato* in CL4) and green (*F. petiolata* and *H. tuna* in CL5) erect algae might be favoured by nutrient availability due to up-welling phenomena (Piazzi et al., 2021) or by a low sediment input that increases light penetration at depth (Doxa et al., 2016; Pierdomenico et al., 2021). CL4 and CL5 encompass few observations ($n = 21$, 10.7%) localized in areas exhibiting peculiar hydrodynamic conditions (such as the western Sardinian side and Montecristo island; Boero et al., 2019) or which are far from river run-off and at a significant distance from the mainland (Pontine and Pianosa islands). Erect bryozoans (*A. calveti*, *M. truncata*, *P. fascialis*, *Reteporella* spp. and *S. cervicornis*) and the yellow gorgonian *E. cavolini* were commonly associated with the aforementioned erect green algae. The observations of CL6 are consistent with each other, showing low intra-cluster silhouette values and uniformly characterized the Ionian basin and some scattered Tyrrhenian SUs. The basal layer was formed mainly by *Peyssonnelia* spp., while the erect algal component mainly consisted of Dictyotales and erect Rhodophyta. As for Ionian basin samples, the invertebrate abundance was scarce and mostly represented by encrusting sponges and the erect bryozoan *P. fascialis*. This is in accordance with the high diversity of sponges and bryozoans, as well as the absence of gorgonian assemblages shallower than 40 m depth that have been reported in the area (Giampaoletti et al., 2020; Longo et al., 2018), and can be explained by the shallow depth interval (25–30 m) at which samples were collected due to the geomorphological features of the studied sites. CL7 displayed a high relative abundance of suspension feeders; the structure of the assemblages was similar to coralligenous dominated by large anthozoans, such as *E. cavolini* and *P. clavata*, reported in both western and eastern Mediterranean Seas (Casas-Güell et al., 2015; Sini et al., 2019). The seafloor morphology of the Gulf of Naples, where Ischia island is located, and the local terrestrial freshwater fluxes enhance the variability of currents along temporal, horizontal and vertical gradients so that they can support the availability of food for the suspension feeder-rich assemblages (de Ruggiero et al., 2016).

It is important to emphasize that the utilization of PAM clustering only partially (i.e., when graphically illustrating the geographic distribution of clusters) conceals the high variability observed at a small spatial scale for coralligenous assemblages. The wide range of *intra*-cluster silhouette values is consistent with spatial variation patterns typical of coralligenous cliffs (Piazzi et al., 2004, 2016; Terlizzi et al., 2007). The choice of considering as SU a set of ten photographs replicated within a 4 m^2 area smoothed the small-scale spatial heterogeneity due to the patchy distribution of species without altering diversity patterns. In fact, the geographic arrangement of PAM clusters is consistent with the high variability of the assemblages reported for the Algero-Provençal and Tyrrhenian ecoregions (Piazzi et al., 2021, 2023). The complexity of geomorphological and hydrodynamic features may shape the variability of coralligenous cliff assemblages when compared to the Ionian ecoregion, as highlighted for shallow littoral and sublittoral areas (Rattray et al., 2016).

The evidence emerging from the study of coralligenous assemblages of the Central-Western Mediterranean fits with the definition of community puzzle given by Ballesteros (2006) and actively contributes to opening new perspectives introducing the metacommunity concept (Leibold et al., 2004), such as a set of regional communities linked by the dispersal of multiple potentially interacting species and characterized by local spatial dynamics. Such an approach was already considered when dealing with the heterogeneity of benthic habitats in the northern Adriatic Sea (Bandelj et al., 2012; Falace et al., 2015) and should be effectively integrated into future studies of coralligenous reefs.

4.2 | Factors shaping diversity patterns

In the study of coralligenous cliffs, geographical distances and depth have been generally used as a proxy for the variation of environmental features over space. The approach we used in this study allowed us to infer about the effect of physico-chemical features, geographic location and connectivity in shaping coralligenous cliffs' diversity patterns.

The α-entropy model estimation provides valuable ecological insights, highlighting how biodiversity patterns are strongly linked to environmental features. The effects of seawater warming and thermal anomalies on benthic communities are increasingly raising concerns among Mediterranean marine ecologists studying coralligenous assemblages (Garrabou et al., 2022). Based on the analysis of water climatology over a 20-year period, excluding temperature anomaly measurements from in situ observations, our results highlight the evidence that elevated temperatures have a detrimental effect on the α-diversity of coralligenous assemblages. As reported by Ceccherelli et al. (2020), variations in median temperature influence the taxonomic richness of the assemblages and lead to distinct responses among benthic taxa. The eastward current speed significantly contributes to shaping α-entropy, unlike the northward component, and increases the diversity of the assemblages. Given the geomorphology of the study area, the currents along the longitudinal axis may generate water movement affecting nutrient and food availability along a coastal-open sea gradient more consistently than along-shore water transfers. The presence of both latitudinal and longitudinal gradients supports the hypothesis on the existence of diversity patterns both among and within ecoregions (Çinar et al., 2020; Doxa et al., 2016; Piazzi et al., 2021, 2023). The α-entropy increases eastward, underlining the urgency of gathering further information in the southern Tyrrhenian and Ionian basins. The U-shaped latitudinal pattern highlighted through the GAM model may be related to the geographical features of the sites located along the continental Tyrrhenian shores (i.e., Latium and Tuscany coasts), where the chlorophyll and nitrate concentrations due to river runoff negatively affect seawater features (Balata et al., 2005; Montefalcone et al., 2017). The composition of coralligenous assemblages is influenced by changes in nutrient concentrations (Ballesteros, 2006; Piazzi et al., 2012). Specifically, an increase in nitrates and phosphates has been found to have a different effect on diversity. Interestingly, phosphate concentration is positively correlated with α-entropy; if compared to nitrates, phosphates are found in lower concentrations in seawater (Garrabou, 1997) and have been identified as predictors in coralligenous occurrence models (Martin et al., 2014).

The analysis of β-entropy, measured at the site level, performed by using GAM reveals the importance of abiotic processes in habitat filtering even in low subtidal environments, where environmental gradients are smoother than in shallower habitats, as indicated by the small variation range of the environmental factors. Temperature enhances variation in the assemblage's structure within sites, acting as a natural stressor that alters the homogeneity of the assemblages at large spatial scales (Casas-Güell et al., 2015; Montefalcone et al., 2017; Piazzi et al., 2016). The effect of northward current speed can be interpreted as a proxy for connection between sites, reflecting the arrangement of observations along the latitudinal gradient. The relationship between β-diversity and environmental variables showed in our study highlighted that high chlorophyll concentrations tend to homogenize coralligenous cliff assemblages. Furthermore, β-diversity revealed different patterns along the latitudinal and longitudinal axes within ecoregions.

GAM and CAR model outputs are consistent with each other; the latter defines a framework in which observations are spatially autocorrelated. The autocorrelation structure defined by the connectivity clusters identified at the largest level of larval dispersal by Andrello et al. (2015) exhibited the highest scores and led the model selection. In parallel, the geographic distance (Euclidean distance around barriers) did not improve the overall explanatory power of the model for β-entropy. This finding is consistent with studies carried out on mesophotic biogenic habitats and sublittoral assemblages in the Adriatic Sea (Bandelj et al., 2020; Rattray et al., 2016). The negative spatial autocorrelation implies that β-diversity exhibits less consistency within clusters and lacks concordance. This results in a wide range of conditions within the same connectivity cluster, with sites that are highly diversified compared to others. However, the CAR model left a consistent proportion of unexplained variance; this could be understood considering further processes, not accounted for in the model and likely acting at a small spatial scale, that shape the diversity patterns within sites. Species interaction or local site features may significantly contribute to shaping β-diversity at the site level. Ignoring biotic interactions (García-Girón et al., 2020), post-settlement processes (Fraschetti et al., 2002), specific information on reproduction and propagule dispersal of the taxa colonizing the reefs (Bandelj et al., 2020; Magris et al., 2016), as well as small-scale morpho-structural and environmental heterogeneity (Bracchi et al., 2016), may undermine our understanding of assembly mechanisms in spatially different areas. Furthermore, biotic interactions and competition for space are significant factors influencing the structure of benthic assemblages, particularly in communities where clonal species are abundant as coralligenous reefs (Ingrosso et al., 2018).

However, it is crucial to emphasize that the connectivity data were derived from an oceanographic model employing a broad spatial resolution and a relatively extended period of larval dispersal (30 days) without considering taxonomic-specific traits. Despite this limitation imposed by the habitat features and the study area extent, the present study highlights the link between connectivity and β-diversity, which is often neglected in Mediterranean biogenic habitats (Bandelj et al., 2020; Ingrosso et al., 2018).

4.3 | Future perspectives in the study of coralligenous cliffs

Coralligenous cliffs are well distributed, algae-dominated, and extremely diversified in the Central-Western Mediterranean Sea. The information provided in this work emphasizes the presence of distinct features according to ecoregions that are influenced by factors such as connectivity and environmental conditions. Temperature, nutrient concentration and current speed were the variables most responsible for the observed patterns.

Coralligenous cliff mapping and surface cover are significantly underestimated. In fact, they cannot be easily identified through remote acoustic methods, and direct sampling can be carried out only in spatially limited areas (Casoli et al., 2021; Martin et al., 2014). The proximity to the coast and the anthropogenic sources of disturbance, the frequency of climate change-related stresses that consistently interest the bathymetric range at which cliffs develop (Garrabou et al., 2022), and the demographic and life-history traits of the structuring species (Montero-Serra et al., 2018) impose a need to discuss our findings from a conservation point of view. The identification of regional patterns in structure and diversity represents the first step to building appropriate monitoring programmes as well as conservation and restoration efforts. Biotic and environmental features should be considered both to highlight degradation in the environmental status and to define reference conditions to avoid biases. The high heterogeneity of coralligenous cliffs that emerged from this study, as recently stated by Piazzi et al. (2023), underscores the importance of treating cliffs and platforms as distinct entities in monitoring programmes, impact assessment studies, and management plans. In this light, the use of diver-based photographic assessments proved to be an effective sampling technique for carrying out community studies and environmental quality assessments in habitats with complex morphology. This method is particularly advantageous compared to the use of remotely operated vehicles (ROVs) or autonomous underwater vehicles (AUVs). Besides being expensive, ROVs and AUVs may face operational and movement limitations when operating in such complex coastal environments.

While this study encompasses a vast geographical coverage within the Central-Western Mediterranean Sea, it underscores the pressing need to assess cliffs developing in regions that have not yet been thoroughly explored. These largely uninvestigated areas encompass the Southern-Eastern Tyrrhenian, Central Ionian and Southern-Western Adriatic Seas. This would allow us to gain a deeper understanding of the endemic coralligenous cliffs, and thus, it is crucial to direct future efforts towards acquiring sampling in these specific locations. Furthermore, it is equally important to investigate diversity patterns and assess the influence of abiotic variables on a broader scale, encompassing the entire Mediterranean basin. In this way, we can improve our spatial planning capability and effectively reach conservation goals, as required by the current EU regulatory framework.

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The authors declare that they have no conflict of interest.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are freely accessible in Zenodo repository at https://doi.org/10.5281/zenodo.10050215 and available upon request from the corresponding author.

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BIOSKETCH

Edoardo Casoli is a researcher in Ecology in the Department of Environmental Biology at Sapienza University of Rome. His research interests involve the structure, dynamics, and conservation of marine benthic communities, especially in the Mediterranean Sea. He primarily examines the ecology and distribution of marine benthic invertebrates, defines patterns of bioconstruction and bioerosion, assesses human impacts and global change effects on marine ecosystems, and develops tools to support marine ecosystem restoration.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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